

Osteology of hyobranchial arches in eurypterygian fishes

Yazdan KEIVANY

*Department of Natural Resources (Fisheries Division), Isfahan University of Technology, Isfahan, 84156-83111, Iran.
Email: keivany@cc.iut.ac.ir*

Abstract: The osteology of the hyoid and branchial arches in several representatives of eurypterygian fishes were examined. The hyoid arches consist of a single basihyal and urohyal, and the arch on each side consists of a dorsal and a ventral hypohyal, an anterior and posterior ceratohyal, an interhyal, and branchiostegal rays that are borne on the ceratohyals. The branchial arches consist of three single, separate, and ossified basibranchials, and in most taxa the arches on each side consist of three hypobranchials, five ceratobranchials, four epibranchials, four pharyngobranchials, and associated teeth and tooth plates. The fourth pharyngobranchial is absent or reduced in all the studied taxa, but the fourth pharyngeal tooth plate is usually present. Gill rakers and small toothplates are present on the branchial arches of most taxa.

Keywords: Bone, Branchial arch, Eurypterygii, Hyoid arch, Osteology.

Introduction

Eurypterygians fishes includes Aulopiformes, Myctophiformes, Lampridiformes, Polymixiiformes, Percopsiformes, Mugiliformes, Atheriniformes, Beloniformes, Cyprinodontiformes, Stephanoberyciformes, Beryciformes, Zeiformes, Gasterosteiformes, Synbranchiformes, Scorpaeniformes, Perciformes, Pleuronectiformes and Tetraodontiformes (Nelson 2006). The hyoid and branchial arches play an important role as skeleton of main respiratory organ, i.e., gills in fishes and therefore, has attracted much attention in ichthyology, both from anatomy and systematics point of views (McAllister 1968; Nelson 1969; Kusaka 1974; Rosen & Patterson 1990). Hence, this study aimed to presents the osteological features of hyoid and branchial arches of representatives of eurypterygian families by describing and illustrating the variable and significant features of the hyoid and branchial arches of selected genera or species. Recently, osteology of the other organs of the eurypterygian fishes have also been studied (e.g., Keivany 2014a, b). The systematics of the taxa follows Eschmeyer (2014) to reflect the new findings in their systematics.

Materials and methods

Representatives of the taxa were cleared and stained following Taylor & Van Dyke (1985) method for osteological examination. A Camera Lucida attached to a Wild M5 dissecting microscope was used to prepare the drawings. The bones in the first figure of each anatomical section are arbitrarily shaded and labeled and in the others are shaded in a consistent manner (dark, medium, and clear) to facilitate comparison among the taxa. Forty five genera representing 40 families were studied. The specimens were obtained from the University of Alberta Museum of Zoology (UAMZ), the Smithsonian Institution (United States National Museum) (USNM), California Academy of Sciences (CAS), and Australian Museum at Sydney (AMS). The number of genera studied in each order is: one in Aulopiformes, Myctophiformes, Lampridiformes, Polymixiiformes, Percopsiformes, Mugiliformes and Elasmobranchiiformes two in Atheriniformes, Beloniformes, Cyprinodontiformes, Stephanoberyciformes, Cetomimiformes, Beryciformes, Zeiformes, Synbranchiformes, four in Scorpaeniformes, five in Perciformes, seven in Syngnathiformes and 10 in

Gasterosteiformes, as follow:

Aulopiformes

Synodontidae: *Synodus synodus* UAMZ 1806.

Myctophiformes

Myctophidae: *Myctophum* sp. UAMZ 2689.

Lampridiformes

Veliferidae: *Velifer hypselopterus* AMS 21839005.

Polymixiiformes

Polymixiidae: *Polymixia lowei* USNM 159300.

Percopsiformes

Percopsidae: *Percopsis omiscomaycus* UAMZ 2048.

Atheriniformes

Atherinidae: *Allanetta harringtonensis* UAMZ 2673.

Melanotaeniidae: *Melanotaenia* sp. UAMZ 3526.

Cyprinodontiformes

Aplocheilidae: *Rivulus hartii* UAMZ 6660.

Cyprinodontidae: *Cyprinodon nevadensis* UAMZ 3114.

Beloniformes

Belonidae: *Pseudotylotus* sp. UAMZ 8165.

Hemiramphidae: *Arrhamphus sclerolepis* UAMZ 3523.

Stephanoberyciformes

Stephanoberycidae: *Stephanoberyx monae* USNM 304353.

Cetomimiformes

Rondeletiidae: *Rondeletia loricata* AMS 20523001.

Zeiformes

Grammicolepididae: *Xenolepidichthys dalgleishi* USNM 322673.

Caproidae: *Antigonia* sp. USNM 266901.

Beryciformes

Monocentridae: *Monocentris* sp. UAMZ 7854.

Holocentridae: *Sargocentron vexillarium* UAMZ 5075.

Incertae sedis

Elassomatidae: *Elassoma zonatum* UAMZ 6920.

Gasterosteiformes

Hypoptychidae: *Hypoptychus dybowskii* UAMZ 5550.

Gasterosteidae:

Spinachia spinachia UAMZ 6582.

Apeltes quadracus UAMZ 7958.

Gasterosteus aculeatus UAMZ 3894.

Culaea inconstans UAMZ 3797.

Pungitius pungitius UAMZ 3049.

Aulorhynchidae:

Aulorhynchus flavidus UAMZ 3783.

Aulichthys japonicus UAMZ 5542.

Indostomidae: *Indostomus paradoxus* UAMZ 6700, CAS 64017.

Pegasidae: *Pegasus volans* UAMZ 4616.

Syngnathiformes

Aulostomidae: *Aulostomus valentini* CAS 11979.

Fistulariidae: *Fistularia petimba* UAMZ 6348.

Centriscidae: *Aeoliscus strigatus* UAMZ 4048.

Macroramphosus scolopax USNM 344398.

Solenostomidae: *Solenostomus paradoxus* AMS 17111002.

Syngnathidae:

Syngnathus scovelli UAMZ 3782.

Syngnathus griseolineatus UAMZ 3469.

Synbranchiformes

Synbranchidae: *Monopterus albus* USNM 192939.

Mastacembelidae: *Macrognathus aculeatus* UAMZ 1625 (120), UAMZ 1855.

Scorpaeniformes

Scorpaenidae: *Sebastes caurinus* UAMZ 3142.

Dactylopteridae: *Dactylopterus volitans* UAMZ 2633.

Hexagrammidae: *Hexagrammos decagrammus* UAMZ 3190.

Agonidae: *Xeneretmus latifrons* UAMZ 3196.

Perciformes

Centrarchidae: *Lepomis gibbosus* UAMZ 7715.4.

Percidae: *Perca flavescens* UAMZ 1244.

Cirrhitidae: *Amblycirrhitis pinos* UAMZ 3640.

Mugilidae: *Mugil* sp. UAMZ 5125.

Pomacentridae: *Stegastes partitus* UAMZ 3640.

Results and Discussion

The hyoid arches consist of an unpaired basihyal and urohyal, and the arch on each side consists of dorsal and ventral hypohyal, anterior ceratohyal, posterior ceratohyal, interhyal, and branchiostegal rays that are

borne on the ceratohyals. As described in the following sections, in some taxa (e.g., Atherinida, Melanotaenidae, Cyprinodontidae, Belonidae, Hemirhamphidae, Caproidae, Gasterosteidae, Pegasidae, Aulostomidae, Fistulariidae, Hexagrammidae, Centrarchidae, Percidae, Mugilidae, Pomacentridae), the anterior ceratohyal is connected to the posterior ceratohyal via medial, lateral or dorsal struts (Figs. 6, 7, 9, 10, 11, 15, 20, 23, 24, 25, 31, 34, 36, 37, 39, 40).

The branchial arches is comprised of three unpaired, separate, and ossified basibranchials, and in most taxa the arches on each side consist of three hypobranchials, five ceratobranchials, four epibranchials, four pharyngobranchials, and associated teeth and tooth plates. A cartilaginous fourth basibranchial is present in many taxa (e.g., Veliferidae, Polymixiidae, Percopsidae, Atherinidae, Melanotaeniidae, Aplocheilidae, Belonidae, Hemiramphidae, Stephanoberycidae, Rondeletiidae, Caproidae, Monocentridae, Holocentridae, Elasmobranchiidae, Gasterosteidae, Aulorhynchidae, Indostomidae, Mastacembelidae, Scorpaenidae, Dactylopteridae, Agonidae, Centrarchidae, Percidae, Cirrhitidae, Mugilidae and Pomacentridae), as described in the following sections (Figs. 3-7, 10, 12, 13, 15-18, 20, 21, 33, 37-40). The third hypobranchial is usually oblique and bears a cylindrical ventral process (Figs. 6, 7, 19, 21, 34, 36-40). Some epibranchials bear an uncinat process (Fig. 18). The first pharyngobranchial is absent (Fig. 8, 11) in some taxa, and when present lacks the pharyngeal tooth plate (Fig. 14). The second and third pharyngobranchials usually bear toothplates (Fig. 18). The fourth pharyngobranchial is absent or reduced in all the studied taxa, but the fourth pharyngeal tooth plate is usually present (Figs. 36-38). Gill rakers and small toothplates are present on the branchial arches of most taxa. McAllister (1968) studied the branchiostegal rays and associated bones, Nelson (1969) studied gill arches, Kusaka (1974) provided a monograph on the urohyal, and Rosen & Patterson (1990) provided an atlas of percomorph

dorsal gill arches. The terminology of Rosen & Patterson (1990) for the hyoid and branchial arches and Rojo (1990) is followed.

Aulopiformes

Synodontidae: *Synodus synodus* (Fig. 1). The basihyal is short and toothed. The urohyal is blade-like, with a dorsal flange. The hypohyals are small and not incorporated in the anterior ceratohyal. The anterior and posterior ceratohyals are thin, deep, and widely separated from each other. The interhyal is cylindrical and relatively long. Eighteen branchiostegal rays are present.

The three basibranchials are fused into a single bone through a dorsal toothplate, and followed by a small cartilaginous element posteriorly. Hypobranchial 3 is much shorter than others. The third and fourth ceratobranchials bear ventral processes, and the fifth one is cylindrical and bears a dorsomedial toothplate. The first epibranchials bears an uncinat process that articulates cartilaginously with the uncinat process of pharyngobranchial 2 and the second bears an uncinat process that articulates with pharyngobranchial 3. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinat process that articulates with epibranchial 1. Pharyngobranchial 3 and 4 bear toothplates.

In *Synodus variegatus*, the uncinat processes of the first epibranchial and the second pharyngobranchial are reduced and do not contact each other. The epibranchials 3 and 4 of *Scopelosaurus* (Notosudidae), epibranchial 3 of *Bathypterois* and *Bathysauropsis* (Ipnopidae), and epibranchial 4 of *Lestrolepis* (Paralepididae) and *Coccorella* (Evermannellidae) bear small uncinat processes (Baldwin & Johnson 1996). In *Pseudotrichonotus* (Pseudotrichonotidae), the basihyal is large, hypohyals are attached to the anterior ceratohyal, branchiostegal rays are six, a fifth cartilaginous epibranchial is present, and pharyngobranchial 2 lacks an uncinat process (Johnson et al. 1996). *Alepisaurus* (Alepisauridae) lacks the first pharyngobranchial and the second

pharyngeal toothplate, and some members of Aulopidae bear a fifth pharyngeal toothplate (Rosen 1973).

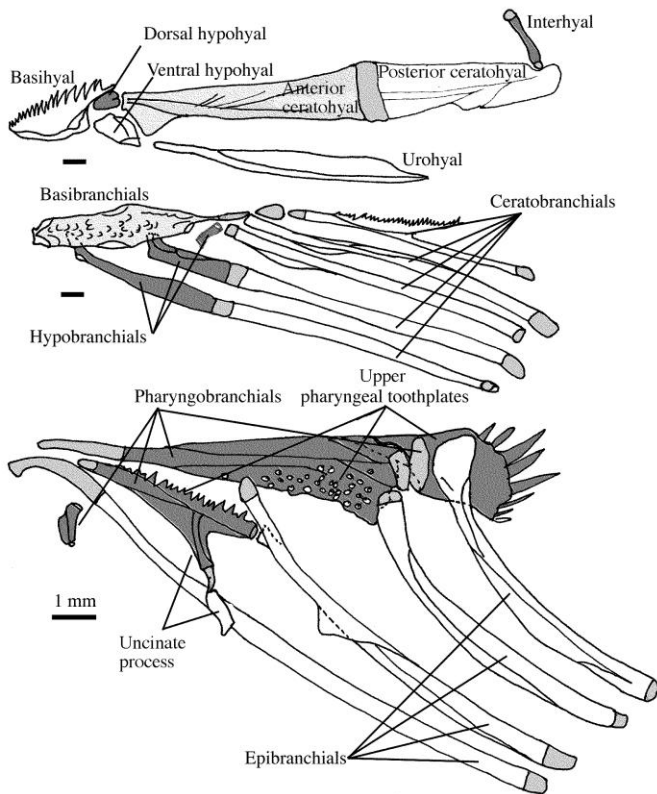


Fig.1. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle), and dorsal (bottom) branchial arches in *Synodus synodus* (UAMZ 1806, 147 mm).

Myctophiformes

Myctophidae: *Myctophum* sp. (Fig. 2). The basihyal is absent. The urohyal is thin and broad. The hypohyals are separated from other elements and bear one branchiostegal ray. The anterior and posterior ceratohyals are thin and broad, and separated from each other. The interhyal is cylindrical. Eight branchiostegal rays are present. The three basibranchials are followed by a cartilaginous element. Basibranchial 2 and 3 are elongated and bear anterior struts that articulate with the preceding basibranchial. Basibranchial 3 is toothed. The third pair of hypobranchials are tightly attached to basibranchial 3 and positioned obliquely ventral to that. The fourth and fifth ceratobranchials bear toothplates. The first epibranchial bears an

uncinate process that articulates via cartilage with the uncinate process of pharyngobranchial 2, the second and the third bear dorsal flanges, and the fourth bears an uncinate process and a dorsal flange. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinate process that articulates with epibranchial 1. Pharyngobranchials 3 and 4 abut each other and bear toothplates. The third epibranchial of some Myctophiformes bear fused toothplates (Stiassny 1996).

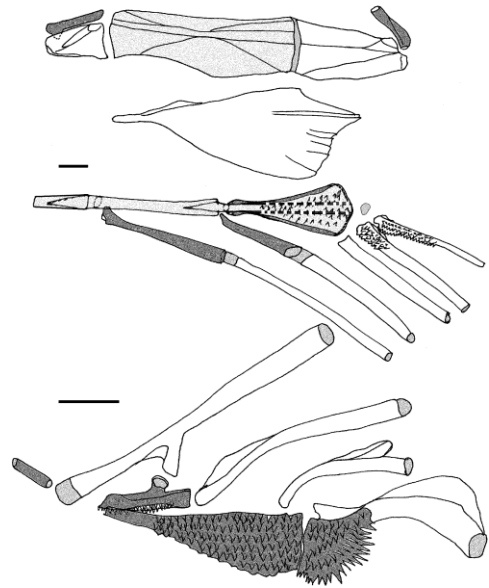


Fig.2. Lateral view of the left hyoid arch (top), dorsal view of the left ventral branchial arches (middle), and ventral view of the dorsal branchial arches (bottom) in *Myctophum* sp. (UAMZ 2689, 60 mm).

Lampridiformes

Veliferidae: *Velifer hypselopterus* (Fig. 3). The basihyal is short. The urohyal is deep and thin. The hypohyals are relatively large and loosely attached to the anterior ceratohyal. The anterior and posterior ceratohyals are short, thin, deep, and separated from each other. The interhyal is cylindrical. Six branchiostegals are present.

The three basibranchials are followed by a cartilaginous element posteriorly. Basibranchial 2 is elongated and bears anterior and posterior struts that articulate with the basibranchial 1 and 3. The fourth ceratobranchial bears a ventral flange and the fifth bears a toothplate. The four short epibranchials,

except epibranchial 2, bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears a short uncinat process that articulates with the first epibranchial uncinat process. Pharyngobranchial 4 is absent, but the fourth pharyngeal toothplate is present. The uncinat process of the fourth epibranchial is absent in Trachipteridae (Rosen 1973). In Lamprididae, the first epibranchial lacks an uncinat process and pharyngeal toothplates are reduced (Olney et al. 1993).

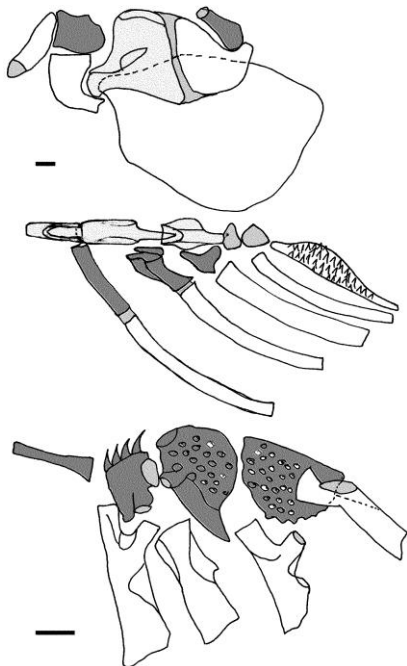


Fig.3. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Velifer hypselopterus* (AMS 21839005, 101 mm).

Polymixiiformes

Polymixiidae: *Polymixia lowei* (Fig. 4). The basihyal is small. The urohyal consists of a bifurcated strut and flanges. The hypohyals are small and loosely attached to the anterior ceratohyal. The anterior and posterior ceratohyals are deep and separated from each other. The interhyal is cylindrical. Four large and two small branchiostegal rays are present.

The three basibranchials are tightly articulated together via cartilage, covered by a single toothplate, and followed by a posteriorly cartilaginous element. The fifth ceratobranchial bears a large toothplate.

The four short epibranchials, except epibranchial 2, bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinat process that articulates with the first epibranchial uncinat process. Pharyngobranchial 4 is absent, but a toothplate is present.

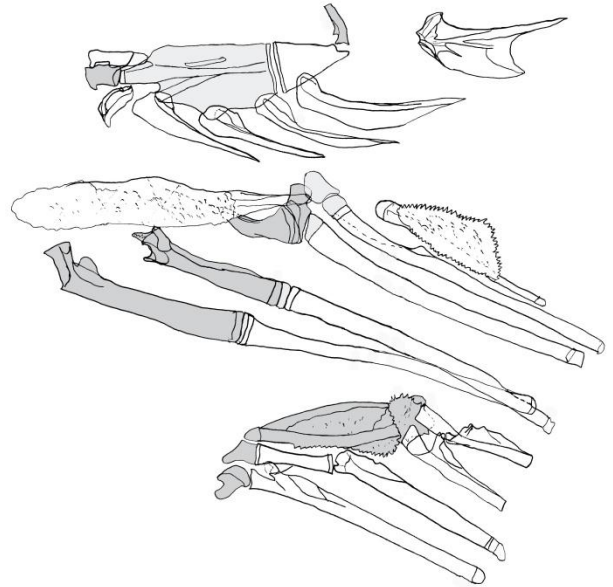


Fig.4. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Polymixia lowei* (USNM 159300 81, 115 mm).

Percopsiformes

Percopsidae: *Percopsis omiscomaycus* (Fig. 5). The basihyal is short. The urohyal consists of a blade and dorsal and ventral flanges. The dorsal hypohyal is incorporated in the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and narrower anteriorly and separated from the posterior ceratohyal. The interhyal is cylindrical. Six branchiostegal rays are present.

The three basibranchials are separated and followed by a cartilaginous element which is covered by a toothplate. The fifth ceratobranchial bears a large toothplate and abut its counterpart for its full length. The four short epibranchials, except epibranchial 2, bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinat process that articulates with the first epibranchial uncinat process.

Pharyngobranchial 4 is absent, but a toothplate is present.

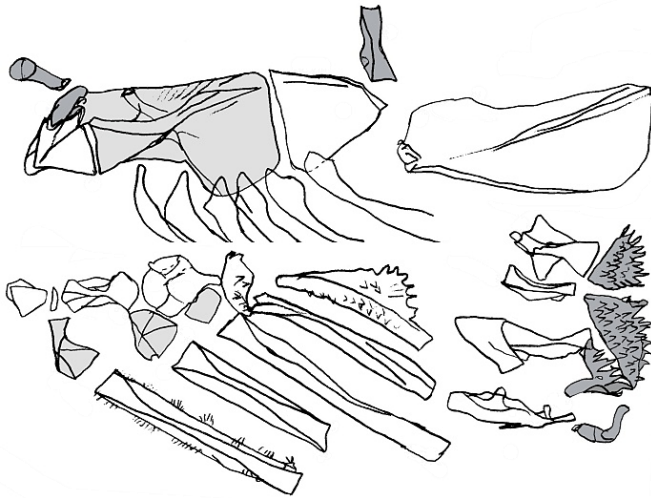


Fig.5. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral and ventral view of dorsal (bottom) branchial arches in *Percopsis omiscomaycus* (UAMZ 2048, 55 mm).

Atheriniformes

Atherinidae: *Allanetta harringtonensis* (Fig. 6). The basihyal is small, but bears a large cartilaginous head anteriorly. The urohyal consists of a small anterodorsal process, a central blade, and ventral and narrow lateral flanges. The hypohyals are small and overlap the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly connecting to the posterior ceratohyal via dorsal struts. The interhyal is small. Six branchiostegal rays are present.

The three basibranchials are covered by thin toothplates and followed by a cartilaginous element. The fifth ceratobranchial bears a large toothplate, and ventral and posterior processes. The four short epibranchials bear uncinat processes and epibranchial 1 and 4 are enlarged. An interarcual cartilage connects the second pharyngobranchial with the first epibranchial. Pharyngobranchial 1 is present. Pharyngobranchial 3 and 4 and their toothplates are fused together. In Phallostethidae, hypohyals are absent or cartilaginous (Parenti 1984) and epibranchials do not bear uncinat processes (Rosen & Parenti 1981).

Melanotaeniidae: *Melanotaenia* sp. (Fig. 7). The

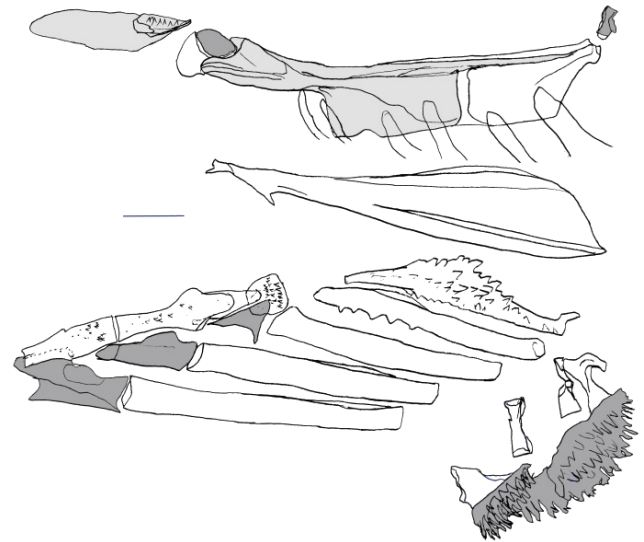


Fig.6. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral and dorsal (bottom) branchial arches in *Allanetta harringtonensis* (UAMZ 2673, 58 mm).

basihyal is small possessing a large cartilaginous head anteriorly. The urohyal consists of an anterodorsal process, a central blade, and ventral and narrow lateral flanges. The hypohyals are small and overlap the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly connecting to the posterior ceratohyal with dorsal struts. The interhyal is very short. Five branchiostegal rays are present.

The three basibranchials are tightly articulated together cartilaginously and followed by a cartilaginous element. The fifth ceratobranchial bears a large toothplate, and ventral and posterior processes. The four short epibranchials, except epibranchial 2, bear uncinat processes and epibranchial 4 is enlarged. An interarcual cartilage connects the second pharyngobranchial with the first epibranchial. Pharyngobranchial 1 is present, pharyngobranchial 3 and 4 are fused together and bear pharyngeal toothplates.

Cyprinodontiformes

Aplocheilidae: *Rivulus hartii* (Fig. 8). The basihyal is short. The urohyal consists of a small anterodorsal process, a central blade, and dorsal, ventral, and lateral flanges. The hypohyals are small and

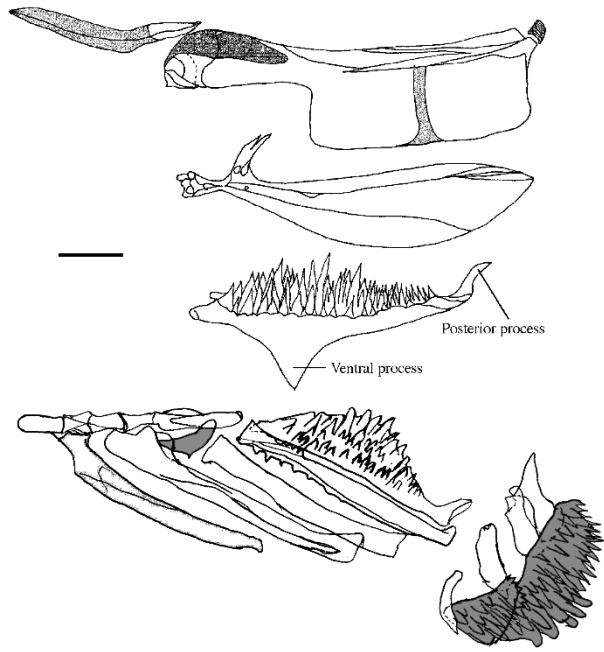


Fig.7. Lateral view of the left hyoid arch (top) and the left fifth ceratobranchial (middle) and dorsal view of ventral branchial arches and ventral view of dorsal branchial arches in *Melanotaenia* sp. (UAMZ 3526, 51 mm).

incorporated in the anterior ceratohyal and positioned beside each other. The anterior ceratohyal is bifurcated anteriorly and each head articulates with one of the hypohyals. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly connecting to the posterior ceratohyal with dorsal struts. The interhyal is small. Seven branchiostegals are present.

The three basibranchials are disk-shaped and followed by a cartilaginous element. The hypobranchials are small and relatively the same size. The fourth ceratobranchial is toothed anteriorly. The fifth ceratobranchial is toothed and bears ventral and posterior processes. The first epibranchial is reduced, the fourth is enlarged, and epibranchials 3 and 4 bear uncinat processes. An interarcual cartilage connects the second pharyngobranchial with the first epibranchial. Pharyngobranchial 1 is absent. Pharyngobranchial 3 and 4 and their toothplates are fused together. The basihyal of *Nothobranchius*, bears a large cartilaginous head, and epibranchial 4 of *Aplocheilichthys panchax* lacks an

uncinate process (Parenti1981).



Fig.8. Dorsal view of the left anterior ceratohyal and hypohyals (top) and the right dorsal branchial arches (bottom) in *Rivulus hartii* (UAMZ 6660, 47 mm).

Cyprinodontidae: *Cyprinodon nevadensis* (Fig. 9). The basihyal is relatively short, but bears an anterior cartilaginous element. The urohyal consists of a small anterodorsal process, a blade, and dorsal and lateral flanges. The hypohyals are small and incorporated in the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly connecting to the posterior ceratohyal via dorsal struts. The interhyal is small. Seven branchiostegal rays are present.

The two basibranchials are long and followed by a cartilaginous element. The hypobranchials are small and relatively the same size. The fourth ceratobranchial is toothed anteriorly and the fifth is toothed and bears ventral and posterior processes. The first epibranchial is reduced, the fourth is enlarged, and epibranchial 3 and 4 bear uncinat

processes. An interarcual cartilage connects the second pharyngobranchial with the first epibranchial. Pharyngobranchial 1 is absent. Pharyngobranchial 3 is moved medially and its toothplate is fused to the fourth toothplate. Pharyngobranchial 4 is reduced, but bears a large fused toothplate. The basihyal of *Cubanichthys* bears a large cartilaginous head and Epibranchial 4 of *Procatopus* (Poeciliidae) lacks an uncinat process (Parenti 1981).

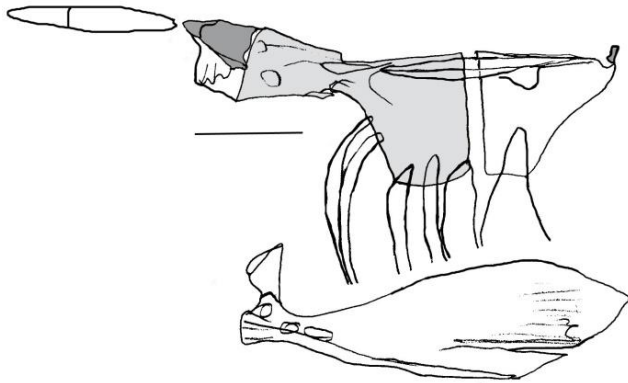


Fig.9. Lateral view of the left hyoid arch (top) and urohyal (bottom) in *Cyprinodon nevadensis* (UAMZ 3114, 34 mm).

Beloniformes

Belonidae: *Pseudotylus* sp. (Fig. 10). The basihyal is small, but bears a large cartilaginous head anteriorly. The urohyal is elongated and consists of a small anterodorsal process and a central blade which trifurcates posteriorly. The hypohyals overlap the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly and connected to the posterior ceratohyal with lateral and medial struts. The interhyal is absent. Eleven branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element. The hypobranchials are short and the third one is tightly connected to the ceratobranchial 3. The fifth ceratobranchials are fused together and toothed. Epibranchials 1-3 bear small processes at their bases and epibranchial 4 is simple and rod-like. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is long and with its toothplate takes place of the epibranchials 3 and 4.

Pharyngobranchial 3 and 4 and their toothplates are absent. Pharyngobranchials 2-4 and a small fourth pharyngeal toothplate are present in *Pseudotylus angusticeps*, *Potamorhaphis*, and *Strongylura*, and pharyngobranchial 2 and its toothplate are present in *Belonion* (Collette 1966).

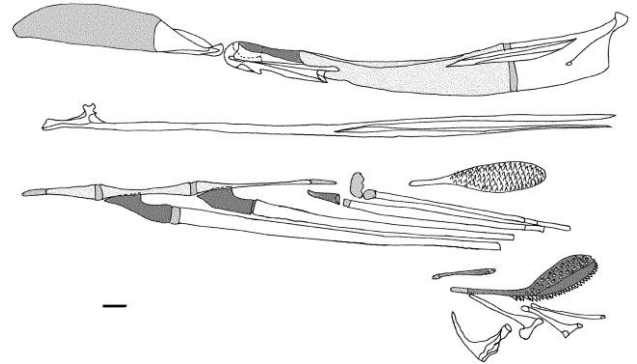


Fig.10. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Pseudotylus* sp. (UAMZ 8165, 173 mm).

Hemiramphidae: *Arrhamphus sclerolepis* (Fig. 11).

The basihyal is small, but bears a large cartilaginous head anteriorly. The urohyal is elongated and consists of a posteriorly bifurcated blade. The hypohyals overlap the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly and connected to the posterior ceratohyal with lateral and medial struts. The interhyal is absent. Twelve branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element. The hypobranchials are relatively short. The ceratobranchials are curved posteriorly functioning as epibranchials. The fifth ceratobranchials are fused together, toothed and bear a ventral process. Epibranchials 2-4 are triradiated and highly reduced, but epibranchial 4 is larger than 2 and 3. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is enlarged and bears a large toothplate. Pharyngobranchials 3 and their toothplates are enlarged and fused together.

Stephanoberyciformes

Stephanoberycidae: *Stephanoberyx monae* (Fig. 12). The basihyal is highly reduced to a small hardly

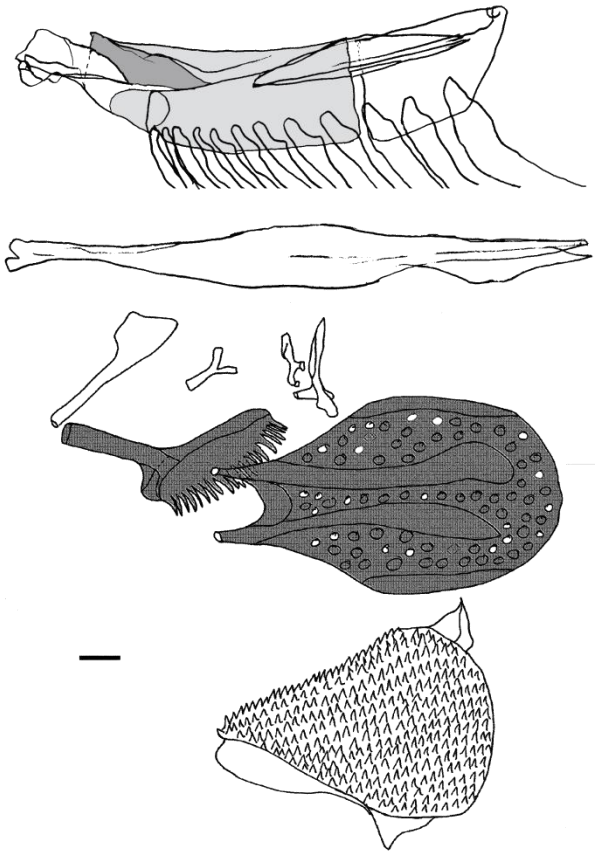


Fig.11. Lateral view of the left hyoid arch and dorsal view of branchial arches (bottom) in *Arrhamphus sclerolepis* (UAMZ 3523, 103 mm).

recognizable cylindrical bone. The urohyal is highly reduced and consists of a bifurcated blade and a flange in between. The hypohyals are not incorporated in the anterior ceratohyal, but overlap the anterior ceratohyal, and are tightly connect to it cartilaginously. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly, separated from the posterior ceratohyal, and bears a small fenestra. The interhyal is cylindrical and relatively long. Eight branchiostegal rays are present.

The three basibranchials are long and followed by a cartilaginous element. The fifth ceratobranchial is reduced and toothless. Epibranchial 1 and 3 bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinat process that articulates with the uncinat process of the first epibranchial, but bears no toothplate. Pharyngobranchial 3 is thin, enlarged, and half of its

surface covered by a toothplate. Pharyngobranchial 4 and its toothplate are reduced.

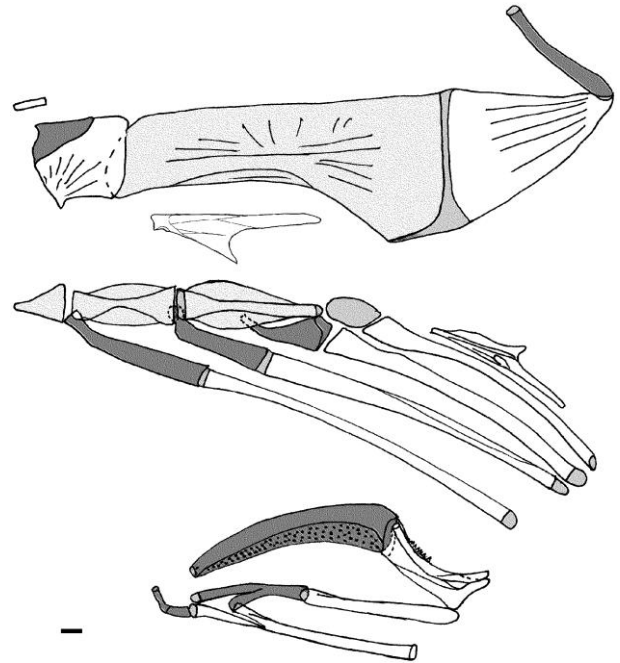


Fig.12. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Stephanoberyx monae* (USNM 304353, 92 mm).

Cetomimiformes

Rondeletiidae: *Rondeletia loricata* (Fig. 13). The basihyal is reduced. The urohyal is highly reduced and consists of a bifurcated blade and a flange in between. The hypohyals are not incorporated in the anterior ceratohyal, but overlap the anterior ceratohyal, and are tightly connect to it cartilaginously. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly, separated from the posterior ceratohyal and bears a small fenestra. The interhyal is cylindrical and relatively long. Eight branchiostegal rays are present.

The three basibranchials are long and followed by a cartilaginous element. The third hypobranchial is smaller, oblique, and its cylindrical ventral process articulates with its counterpart ventrally. The fifth ceratobranchial is reduced and toothless. Epibranchial 1, 3 and 4 bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinat process that articulates with the

uncinate process of the first epibranchial without toothplate. Pharyngobranchial 3 is thin, enlarged, and half of its surface covered by a toothplate. Pharyngobranchial 4 and its toothplate are reduced.

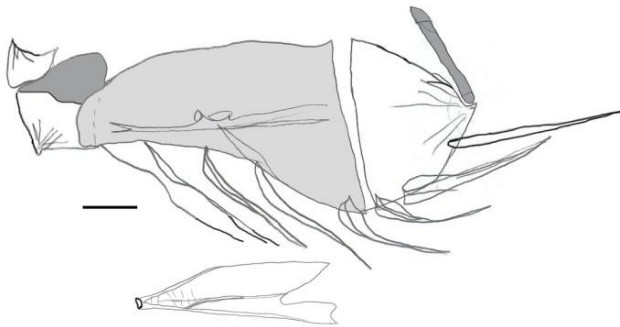


Fig.13. Lateral view of the left hyoid arch in *Rondeletia loricata* (AMS 21141001, 37 mm).

Zeiformes

Grammicolepididae: *Xenolepidichthys dalgleishi* (Fig. 14). The basihyal is enlarged and articulates with the second basibranchial. The urohyal consists of a blade and a dorsal flange. The hypohyals are relatively large, not incorporated in the anterior ceratohyal, but overlap the anterior ceratohyal, and are connect to it cartilaginously. The anterior ceratohyal is short, and deep, separated from the posterior ceratohyal and bears two fenestrae. The interhyal is cylindrical and relatively long. Seven branchiostegal rays are present.

The three basibranchials are long, the second is bent ventrally and at the bending point articulates with the basihyal and bears anterior and posterior struts that covers the first and third basibranchials. The first basibranchials is positioned ventral to the basihyal. The fifth ceratobranchial is reduced and toothless. Epibranchials 2-4 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 and 3 and their toothplates are reduced. Pharyngobranchial 4 and its toothplate are absent.

Caproidae: *Antigonia* sp. (Fig. 15). The basihyal is moderate. The urohyal consists of a bifurcated blade, a dorsal flange, and a flange between the blades. The hypohyals are relatively large but not incorporated in the anterior ceratohyal. The anterior ceratohyal is short, deeper posteriorly and gradually becomes

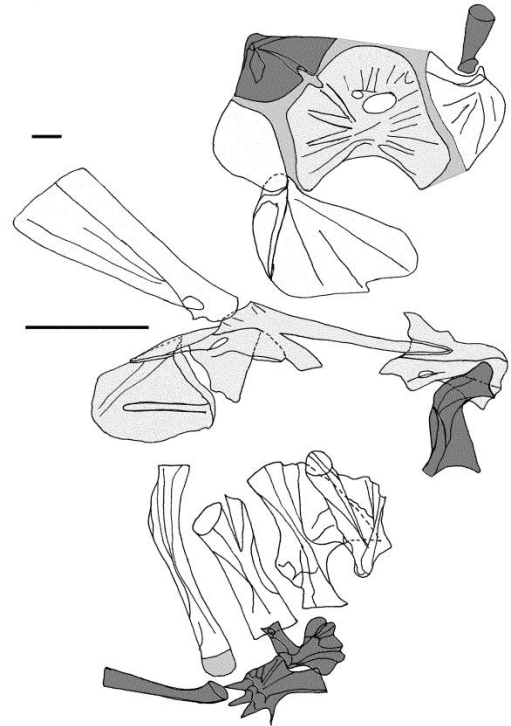


Fig.14. Lateral view of the left hyoid arch (top), basihyal and basibranchials (middle), and ventral view of the left dorsal branchial arches (bottom) in *Xenolepidichthys dalgleishi* (USNM 322673, 68 mm).

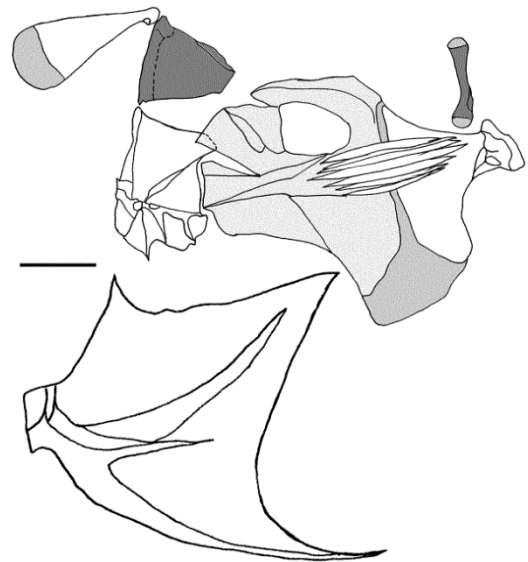


Fig.15. Lateral view of the left hyoid arch in *Antigonia* sp. (USNM 266901, 37 mm).

narrower anteriorly, bifurcated anteriorly and each fork receives a hypohyal. The anterior ceratohyal is connected to the posterior ceratohyal by lateral struts, and bears a fenestra. The interhyal is cylindrical and relatively long. Six branchiostegal rays are present.

The three basibranchials are long and followed by a small cartilaginous element. The fifth ceratobranchial is toothed. Epibranchial 1, 3 and 4 bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 and 3 and their toothplates are reduced. Pharyngobranchial 4 is absent, but a small toothplate is present. In *Antigoniacapros*, a small fourth pharyngobranchial is present (Rosen 1984).

Beryciformes

Monocentridae: *Monocentris* sp. (Fig. 16). The basihyal is reduced. The urohyal consists of a blade and dorsal and ventral flanges. The hypohyals are not incorporated with the anterior ceratohyal, but overlap the anterior ceratohyal that are tightly connected cartilaginously. The anterior ceratohyal is short and deeper posteriorly, and gradually becomes narrower anteriorly, separated from the posterior ceratohyal and bears a fenestra. The interhyal is cylindrical and relatively long. Eight branchiostegal rays are present.

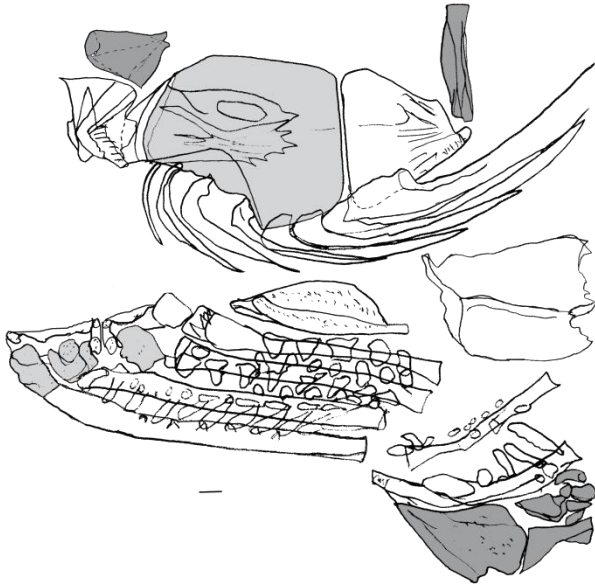


Fig.16. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Monocentris* sp. (UAMZ 7854, 92 mm).

The three basibranchials are long and followed by a cartilaginous element. The third hypobranchial is oblique, tightly connected to the third basibranchial, and its long cylindrical ventral process articulates with its counterpart ventrally. The fifth

ceratobranchial is toothed. Epibranchial 1, 3 and 4 bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinat process that articulates with the uncinat process of the first epibranchial, but bears no toothplate. Pharyngobranchial 3 bears a toothplate, but epibranchial 4 and its toothplate are absent.

Holocentridae: *Sargocentron vexillarium* (Fig. 17). The basihyal is relatively long. The urohyal consists of a blade and a dorsal flange. The hypohyals are not incorporated in the anterior ceratohyal, but overlap the anterior ceratohyal, and are tightly connected to it cartilaginously. The anterior ceratohyal is short, deeper posteriorly and gradually becomes narrower anteriorly, separated from the posterior ceratohyal and bears a fenestra. The interhyal is cylindrical and relatively long. Eight branchiostegal rays are present.

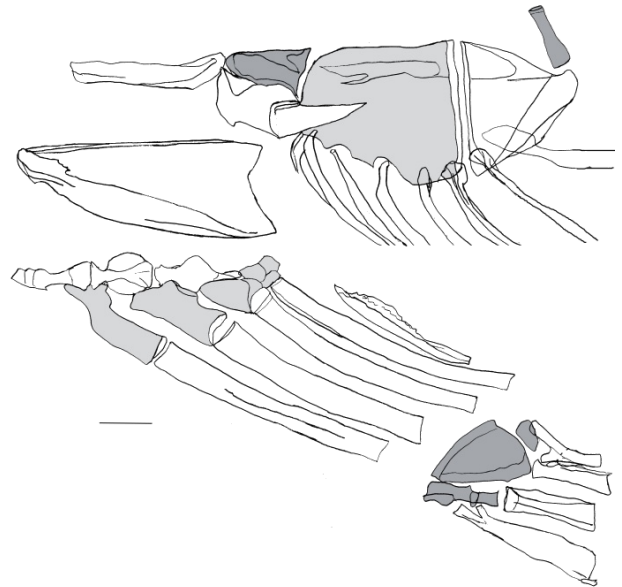


Fig.17. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Sargocentron vexillarium* (UAMZ 5075, 44 mm).

The three basibranchials are long and followed by a cartilaginous element. The fifth ceratobranchial is toothed. Epibranchial 1, 3 and 4 bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 without toothplate and bears an uncinat process that articulates with the uncinat process of the first epibranchial. Pharyngobranchial 3 is large and bears a toothplate. Pharyngobranchial

4 is absent, but a toothplate is present.

Incertae sedis

Elassomatidae: *Elassoma zonatum* (Fig. 18). The basihyal is flattened. The urohyal consists of an anterodorsal process, a posteriorly bifurcated blade and a flange in between, and narrow ventrolateral flanges. The hypohyals overlap the anterior ceratohyal and the dorsal hypohyal bears a fenestra. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly, is separated from the posterior ceratohyal, but tiny medial struts are present. The interhyal is cylindrical. Five branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element. The hypobranchials are short. The fifth ceratobranchial is toothed and bears a small ventral flange. Epibranchial 3 bears an uncinat process. Pharyngobranchial 1 is absent. Pharyngobranchial 2 bears a small toothplate. Pharyngobranchial 4 is absent, but a small toothplate is present.

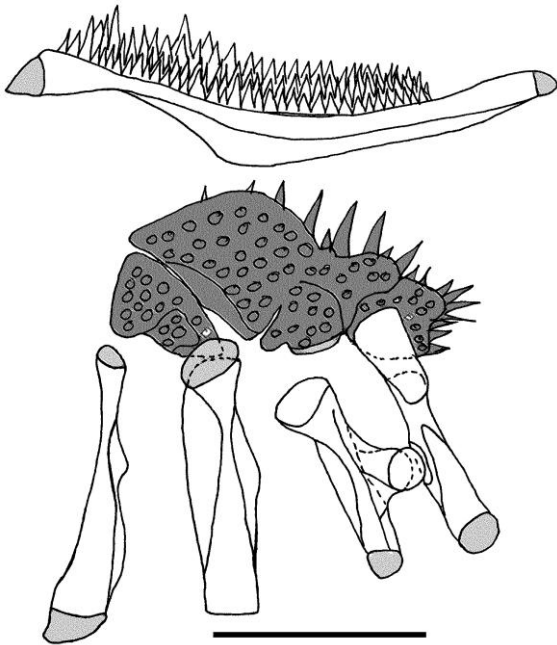


Fig.18. Lateral view of the left fifth ceratobranchial (top) and dorsal view of the left dorsal branchial arches (bottom) in *Elassoma zonatum* (UAMZ 6920, 30 mm).

Gasterosteiformes

Hypoptychidae: *Hypoptychus dybowski* (Fig. 19). The basihyal is elongated. The urohyal is long and

consists of a blade, a posteriorly fimbriated dorsal flange, and ventrolateral flanges. The hypohyals are small and incorporated in the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly and separated from the posterior ceratohyal. The interhyal is small. Four branchiostegal rays are present.

The three basibranchials are long and cylindrical. The fifth ceratobranchial is toothless, cylindrical, and the same length as the others. Epibranchial 3 and 4 are reduced and bear uncinat processes. Pharyngobranchial 1 and 4 are absent. Pharyngobranchials 2 and 3 are long and cylindrical and bear few teeth.

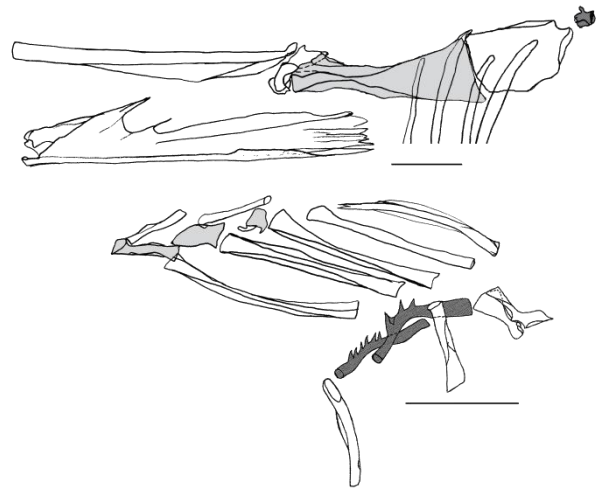


Fig.19. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Hypoptychus dybowski* (UAMZ 5550, 80 mm).

Gasterosteidae: *Apeltes quadracus* (Fig. 20). The basihyal is elongated in *Spinachia spinachia* and moderate in others. The urohyal is long in *S. spinachia*, moderate in others and consists of a blade, a dorsal flange, and ventrolateral flanges. The hypohyals are small and incorporated in the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly, and is connected to the posterior ceratohyal by dorsal struts. The interhyal is cylindrical. Three branchiostegal rays are present.

The three basibranchials are long and followed by a cartilaginous element. The hypobranchials are

roundish and the third one is oblique. The fifth ceratobranchial is toothed. Epibranchial 4 is long and like that of epibranchial 3 bears an uncinat process. Pharyngobranchial 1 is absent. Pharyngobranchial 2 and 3 bear toothplates. Pharyngobranchial 4 and its toothplate are absent.

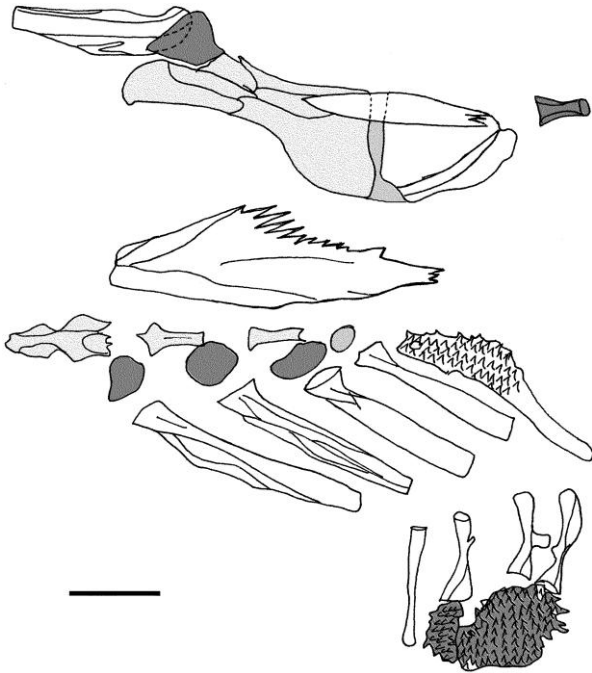


Fig.20. Lateral view of the left hyoid arch (top), dorsal view of the left ventral branchial arches (middle), and ventral view of the left dorsal branchial arches (bottom) in *Apeltes quadracus* (UAMZ 7958, 37 mm).

Aulorhynchidae: *Aulichthys japonicus* (Fig. 21). The basihyal is elongated. The urohyal is long and consists of a blade, a dorsal flange, and posteriorly expanded (and fimbriated in *Aulorhynchus flavidus*) ventrolateral flanges. The hypohyals are small and incorporated in the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly and is separated from the posterior ceratohyal. The interhyal is present. Four branchiostegal rays are present.

The three basibranchials are long and cylindrical and followed by a cartilaginous element in *Aulorhynchus flavidus*. The fifth ceratobranchial is cylindrical and toothed. Epibranchial 4 is long and like that of epibranchial 3 bears an uncinat process.

Pharyngobranchial 1 is absent. Pharyngobranchial 2 and 3 and their toothplates are large. Pharyngobranchial 4 is absent, but a toothplate is present in *A. flavidus*.

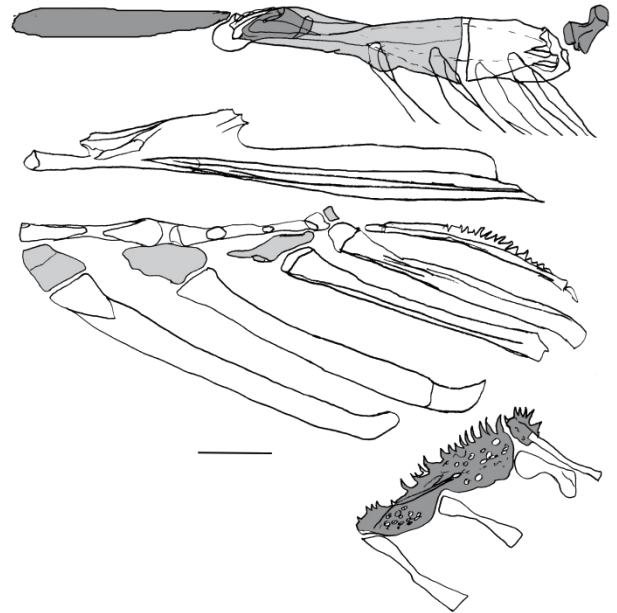


Fig.21. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Aulichthys japonicus* (UAMZ 5542, 47 mm).

Indostomidae: *Indostomus paradoxus* (Fig. 22). The basihyal is enlarged. The urohyal consists of a posteriorly bifurcated blade and a dorsal flange. The hypohyals are highly incorporated in the anterior ceratohyal. The anterior ceratohyal is tightly connected to the posterior ceratohyal. The interhyal is small. Six branchiostegal rays are present.

The three basibranchials are followed by a large cartilaginous element. The hypobranchials are rectangular. Ceratobranchials 4 and 5 are toothed. Epibranchials bear no uncinat processes and epibranchial 4 is slightly enlarged. Pharyngobranchial 1 and 2 are absent. Pharyngobranchial 4 is absent, but a toothplate is present. Gill filaments are lophobranch with skeleton fused basally. Also see Banister (1970).

Pegasidae: *Pegasus volans* (Fig. 23). The basihyal is moderate. The urohyal consists of a bifurcated blade, a flange in between, and narrow ventrolateral flanges.

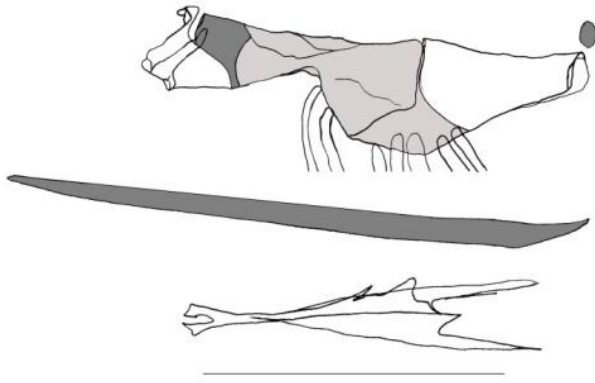


Fig.22. Lateral view of the left hyoid arch (top), and basihyal (middle) and dorsal view of urohyal (bottom) in *Indostomus paradoxus* (CAS 64017, 25 mm).

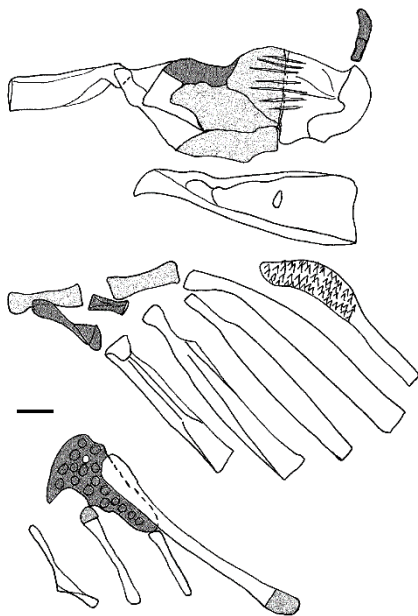


Fig.23. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Pegasus volans* (UAMZ 4616, 99 mm).

The hypohyals are relatively large and incorporated in the anterior ceratohyal. The anterior ceratohyal is deep and connected to the posterior ceratohyal by lateral struts. The interhyal is cylindrical. Five filamentous branchiostegal rays are present.

The two basibranchials are long. The third hypobranchial is absent. The fifth ceratobranchial is toothed. Epibranchial 4 is elongated and like that of epibranchials 1-3 lacks an uncinat process. Pharyngobranchial 1 is absent. Pharyngobranchial 2 bears a toothplate. Pharyngobranchial 3 and 4 and

their toothplates are absent. Gill filaments are lophobranch with skeleton fused basally as described by Johnson & Patterson (1993).

Syngnathiformes

Aulostomidae: *Aulostomus valentini* (Fig. 24). The basihyal is elongated. The urohyal is an elongated and posteriorly deepened blade. The hypohyals are highly incorporated into the anterior ceratohyal and the ventral hypohyal is large and articulated with the posterior ceratohyal. The anterior ceratohyal is tightly connected to the posterior ceratohyal and bears a small fenestra. The posterior ceratohyal bears medial and lateral extensions that articulate with anterior ceratohyal and ventral hypohyal. The interhyal is large and triangular. Four branchiostegal rays are present.

Basibranchial 2 and 3 are absent. The hypobranchials are short, hourglass shaped, and the third hypobranchial consists only of a ventral cylindrical process. The fifth ceratobranchial is reduced, cylindrical, and bears a toothplate. Epibranchial 1 bears an uncinat process and epibranchial 4 is absent. Pharyngobranchial 1 is absent. Pharyngobranchial 2 and 3 are cylindrical, long, and bear toothplates. Pharyngobranchial 4 is absent, but a toothplate is present.

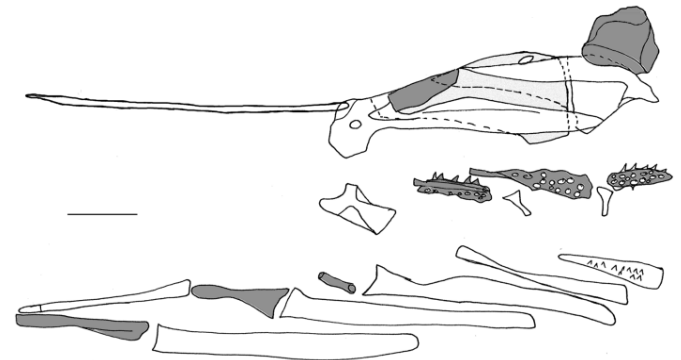


Fig.24. Lateral view of the left hyoid arch (top), and dorsal view of the left dorsal (middle) and ventral (bottom) branchial arches in *Aulostomus valentini* (CAS 11979, 139 mm).

Fistulariidae: *Fistularia petimba* (Fig. 25). The basihyal is elongated. The urohyal is elongated and consists of a posteriorly bifurcated blade. The hypohyals are tightly articulated with the anterior

ceratohyal and the ventral hypohyal articulates with the posterior ceratohyal. The anterior ceratohyal is tightly connected to the posterior ceratohyal by strong struts. The interhyal is fused to the posterior ceratohyal. Five branchiostegal rays are present.

Basibranchial 2 and 3 are absent. The hypobranchials are small. The fifth ceratobranchial is reduced, cylindrical, and toothless. Epibranchial 1 bears an uncinat process and epibranchial 4 is absent. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is cylindrical, long, and bears a toothplate. Pharyngobranchial 3 and 4 are absent, but toothplates are present. No gill rakers are present on the branchial arches.

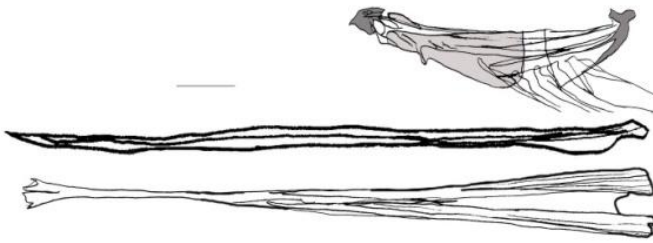


Fig.25. Lateral view of the left hyoid arch (top), and lateral (middle) and dorsal view of urohyal (bottom) in *Fistularia petimba* (UAMZ 6348, 158 mm).

Macroramphosidae: *Macroramphosus scolopax* (Fig. 26). The basihyal is elongated. The urohyal is elongated and consists of a posteriorly trifurcated blade and a ventral flange. The hypohyals are tightly articulated with the anterior ceratohyal and the ventral hypohyal is enlarged. The anterior ceratohyal is separated from the posterior ceratohyal. The posterior ceratohyal is reduced. The interhyal is relatively large, round, and sutured in a notch posterodorsal to the posterior ceratohyal. Four short branchiostegal rays are present.

Basibranchial 1 is fused to the basihyal and a cartilaginous element follows the third basibranchial. Hypobranchials bear short ventral processes. The fifth ceratobranchial is reduced, cylindrical, and toothed. Epibranchial 1 is highly enlarged and epibranchials 1-4 bear uncinat processes. Pharyngobranchial 1 is absent. Pharyngobranchials 2-4 and their toothplates are reduced.

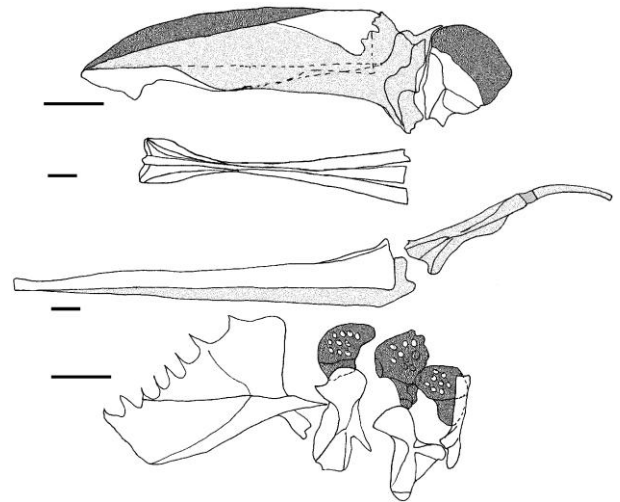


Fig.26. Lateral view of the left hyoid arch and dorsal view of the urohyal (top), lateral view of the basihyal and basibranchials (middle), and dorsal view of the left dorsal branchial arches (bottom) in *Macroramphosus scolopax* (USNM 344398, 99 mm).

Centriscidae: *Aeoliscus strigatus* (Fig. 27). The basihyal is elongated and depressed. The urohyal is elongated and consists of a posteriorly bifurcated blade and a dorsal flange. The hypohyals are tightly articulated with the anterior ceratohyal. The ventral hypohyal is the largest element, embraces the anterior ceratohyal, and articulates with the posterior ceratohyal. The anterior ceratohyal is tightly connected to the posterior ceratohyal. The interhyal is relatively large and round, and sutured in a notch posterior to the posterior ceratohyal. Four filamentous and elongated branchiostegal rays are present.

Basibranchial 1 is fused to the basihyal. The third hypobranchial bears a short ventral process. The fifth ceratobranchial is cylindrical and toothed. Epibranchial 3 and 4 bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 and 3 bear toothplates. Pharyngobranchial 4 is absent, but a toothplate is present. For further information on this order, see Bowne (1985, 2000), Orr (1995), Keivany (1996, 2000) Keivany et al. (1997), Keivany & Nelson (1998, 2000) and Takata & Sasaki (2005).

Solenostomidae: *Solenostomus paradoxus* (Fig. 28). The basihyal is absent. The urohyal is elongated and

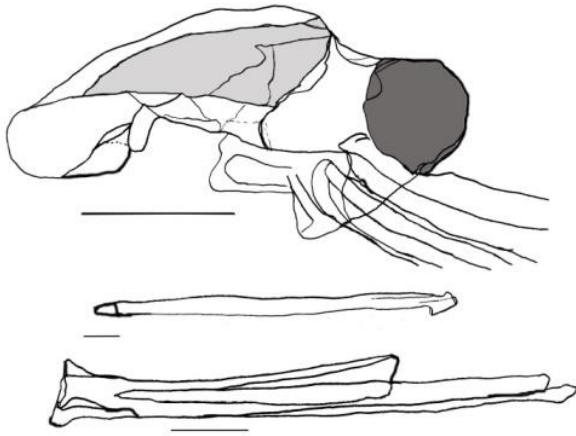


Fig.27. Lateral view of the left hyoid arch (top), and basihyal (middle) and urohyal (bottom) in *Aeoliscus strigatus* (UAMZ 4048, 89 mm).

consists of a posteriorly bifurcated blade. The hypohyals are incorporated into the anterior ceratohyal. The anterior ceratohyal is elongated and separated from the posterior ceratohyal. The posterior ceratohyal is reduced. The interhyal is small, cylindrical, and located in a notch posterior to the posterior ceratohyal. One bifurcated, filamentous, and elongated branchiostegal ray is present.

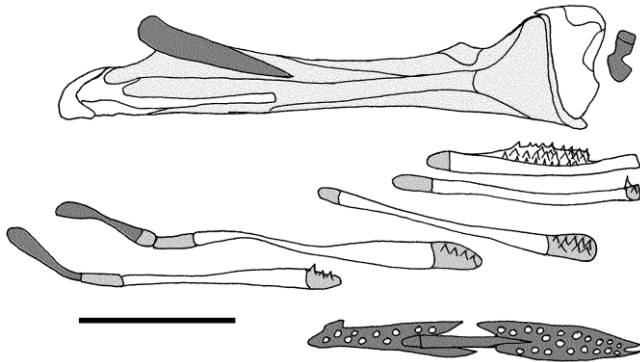


Fig.28. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and the dorsal (bottom) branchial arches in *Solenostomus paradoxus* (AMS 17111002, 51 mm).

Basibranchials and the third hypobranchial are absent. The fifth ceratobranchial is cylindrical and toothed. Epibranchials are absent. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is absent, but a toothplate is present. Pharyngobranchial 3 bears a long toothplate. Pharyngobranchial 4 and its toothplate are absent. No gill rakers are present on the branchial arches, but few small teeth are present on

the cartilaginous distal end of the ceratobranchials (epibranchials of Orr (1995)). Gill filaments are lophobranch with skeleton fused basally.

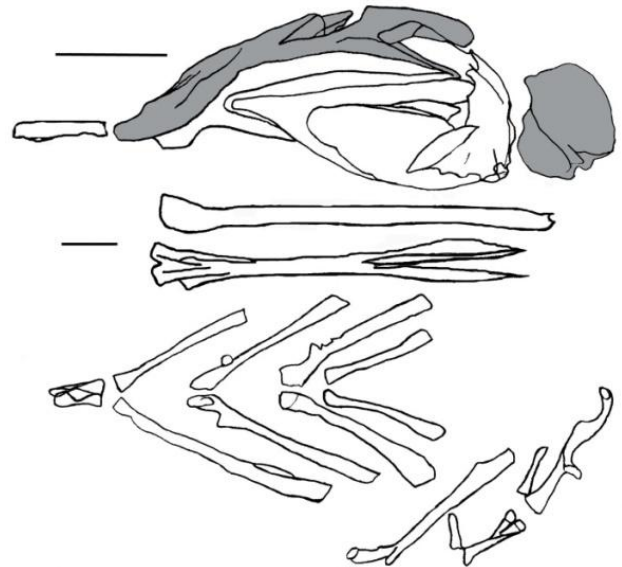


Fig.29. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Hippocampus ingens* (UAMZ 3594, 170 mm).

Syngnathidae: *Hippocampus ingens* (Fig. 29). The basihyal is short and cylindrical. The urohyal is elongated and consists of a posteriorly bifurcated blade. The hypohyals are tightly incorporated in the anterior ceratohyal and the ventral hypohyal is the largest element and embraces the anterior ceratohyal and articulates with the posterior ceratohyal. The anterior ceratohyal is tightly connected to the posterior ceratohyal. The interhyal is relatively large and round, and located in a notch posterior to the posterior ceratohyal. Two filamentous and elongated branchiostegal rays are present.

Basibranchials 2 and 3 are absent. Hypobranchial 1 and 2 are long and hypobranchial 3 is absent. Ceratobranchials 3-5 are angled and bear ventral processes at their angling point. The fifth ceratobranchial is cylindrical and toothless. Epibranchial 4 is absent. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is cylindrical and pharyngobranchial 3 bears an uncinat process. All the toothplates are absent. Gill filaments are lophobranch with skeleton fused basally.

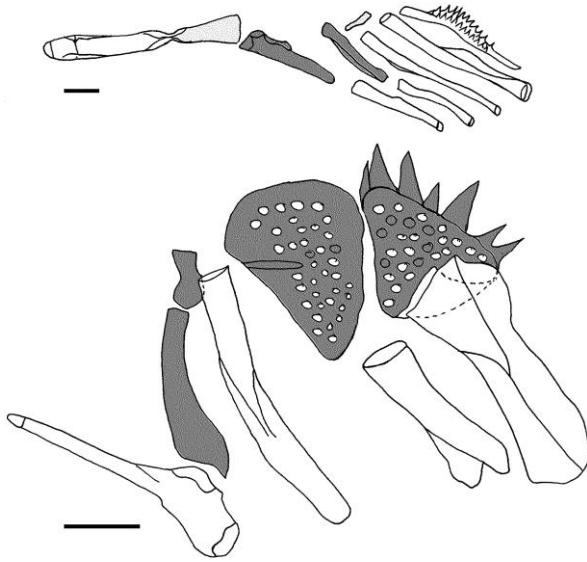


Fig.30. Dorsal view of the left ventral (top) and dorsal branchial arches (bottom) in *Monopterus albus* (USNM 192939, 193 mm).

Synbranchiiformes

Synbranchidae: *Monopterus albus* (Fig. 30). The basihyal is cylindrical, long, and fused to the first basibranchial. The urohyal is long, anteriorly depressed, and consists of a strong blade. The hypohyals are incorporated in the anterior ceratohyal. The anterior ceratohyal becomes abruptly narrower anteriorly and is connected to the posterior ceratohyal by strong struts. The interhyal is long. Six branchiostegal rays are present.

The first basibranchial is fused to the basihyal and basibranchial 2 and 3 are absent. The hypobranchials are long and the third one consists of only a small cylindrical ventral process. The fifth ceratobranchial is cylindrical and toothed. An interarcual bone that connects epibranchial 1 to pharyngobranchial 2 is present. Epibranchial 3 bears an uncinat process and epibranchial 4 is enlarged. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is small and cylindrical. Pharyngobranchial 3 and 4 are absent, but toothplates are present. No gill rakers are present on the branchial arches.

In *Macropterna*, *Ophisternon* and *Synbranchus*, basibranchial 2 and 3 are present. In *Monopterus boueti*, *M. cuchia*, and some specimens of *M. albus*, a vestigial basibranchial 2 is present. In *Monopterus*

cuchia, the first epibranchial is absent and others lack the uncinat processes. In *Ophisternon* and *Synbranchus*, the fourth epibranchial bears an uncinat process and pharyngobranchial 3 is present (Rosen & Greenwood 1976). Also see Britz & Kottelat (2003).

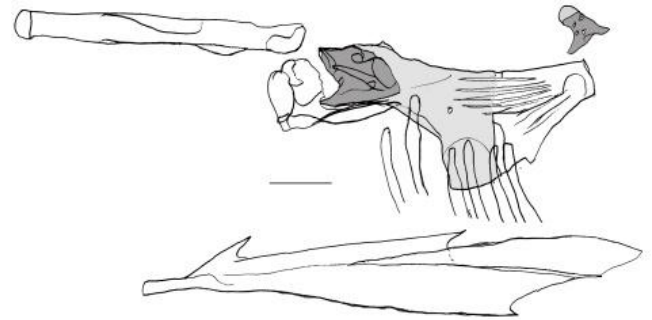


Fig.31. Lateral view of the left hyoid arch (top), and urohyal (bottom) in *Macrognathus aculeatus* (UAMZ 1855, 119 mm).

Mastacembelidae: Macrognathus aculeatus (Fig. 31).

The basihyal is cylindrical and long. The urohyal is long and consists of a blade and a bifurcated dorsal flange. The hypohyals are incorporated into the anterior ceratohyal. The anterior ceratohyal becomes abruptly narrower anteriorly and is connected to the posterior ceratohyal by strong struts. The interhyal is small. Six branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element. The first basibranchial is fused to the basihyal. The hypobranchials are short and all bear cylindrical ventral processes. The fifth ceratobranchial is toothed. Epibranchial 3 and 4 bear uncinat processes. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is absent, but a small toothplate is present. Pharyngobranchial 3 and a small pharyngobranchial 4 and their toothplates are present. No gill rakers are present on the branchial arches.

Scorpaeniformes

Scorpaenidae: *Sebastes caurinus* (Fig. 32). The basihyal is cylindrical. The urohyal is shorter than the hyoid arch and consists of a blade and a dorsal flange. The hypohyals are not tightly articulated with the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly

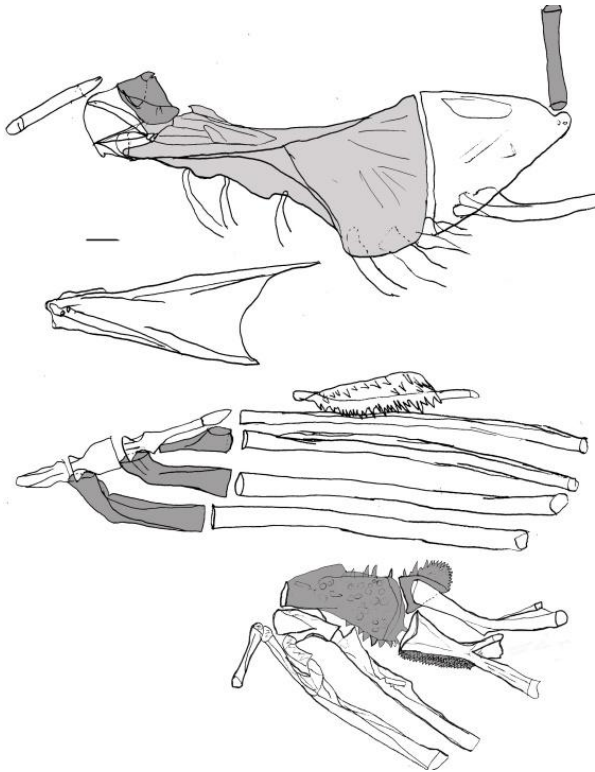


Fig.32. Lateral view of the left fourth and fifth ceratobranchials (top) and dorsal view of the left dorsal branchial arches (bottom) in *Sebastes caurinus* (UAMZ 3142, 75 mm).

and is separated from the posterior ceratohyal. The interhyal is cylindrical and long. Seven branchiostegal rays are present.

The three cylindrical basibranchials are followed by a cartilaginous element. Hypobranchial 1 is angled and hypobranchial 3 is oblique and bears a cylindrical ventral process. The fourth ceratobranchial bears a ventral process. The fifth ceratobranchial is toothed and expanded anteroventrally. Epibranchial 1, 3 and 4 bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears a small toothplate, an uncinat process, and is connected to the first epibranchial by an interarcual cartilage. Pharyngobranchial 4 is absent, but a small toothplate is present.

Dactylopteridae: *Dactylopterus volitans* (Fig. 33). The basihyal is cylindrical. The urohyal is small and consists of a bifurcated blade and a flange in between. The hypohyals are incorporated into the anterior

ceratohyal. The anterior ceratohyal is hourglass shaped and separated from the posterior ceratohyal. The interhyal is cylindrical and long. Six branchiostegal rays are present.

The three cylindrical basibranchials are followed by a cartilaginous element. The hypobranchials are short and all are oblique and bear cylindrical ventral processes. The fifth ceratobranchial is toothed. Epibranchial 1, 3 and 4 bear uncinat processes. Pharyngobranchial 1 is cartilaginous. Pharyngobranchial 2 bears a small toothplate. Pharyngobranchial 4 is absent, but a small toothplate is present.

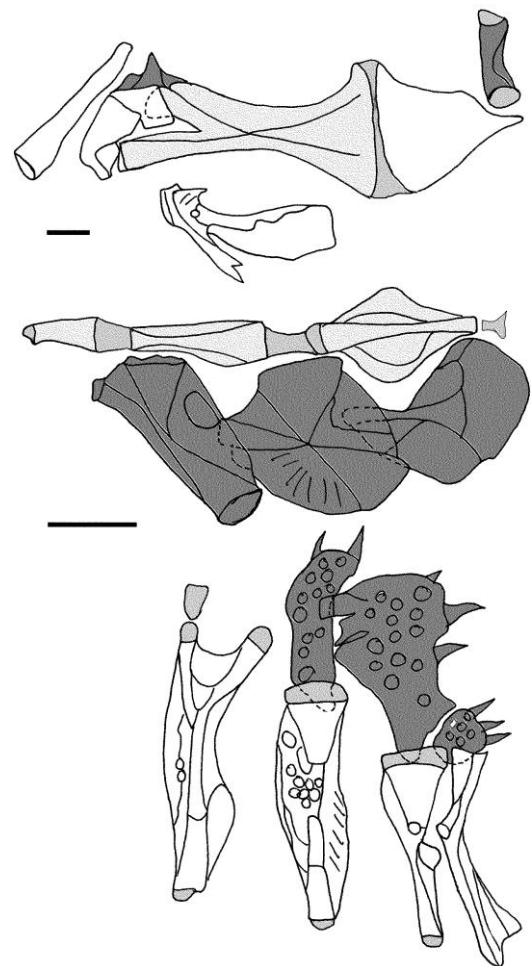


Fig.33. Lateral view of the left hyoid arch (top), dorsal view of the basibranchials and left hypobranchials (middle), and dorsal view of the dorsal branchial arches (bottom) in *Dactylopterus volitans* (UAMZ 2633, 74 mm).

Hexagrammidae: *Hexagrammos decagrammus* (Fig. 34). The basihyal is depressed. The urohyal is shorter



Fig.34. Lateral view of the left fourth and fifth ceratobranchials (top) and dorsal view of the left dorsal branchial arches (bottom) in *Hexagrammos decagrammus* (UAMZ 3190, 50 mm).

than the hyoid arch and consists of a blade, an anterodorsal process, and a dorsal flange. The hypohyals are not tightly articulated with the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly, and is connected to the posterior ceratohyal by small medial struts. The interhyal is cylindrical and long. Six branchiostegal rays are present.

Three cylindrical basibranchials are present. The hypobranchials are short. The fifth ceratobranchial is cylindrical and toothed. The fourth epibranchial is slightly larger than 2 and 3. Epibranchial 1, 3, and 4 bear uncinat processes. Pharyngobranchial 1 is absent. Pharyngobranchial 2 bears a small toothplate. Pharyngobranchial 4 is absent, but a small toothplate is present.

Agonidae: *Xeneretmus latifrons* (Fig. 35). The basihyal is absent. The urohyal is shorter than the hyoid arch and consists of a blade, a dorsal flange,

and broad ventrolateral flanges. The hypohyals are not tightly articulated with the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly and is separated from the posterior ceratohyal. The interhyal is cylindrical and long. Six branchiostegal rays are present.

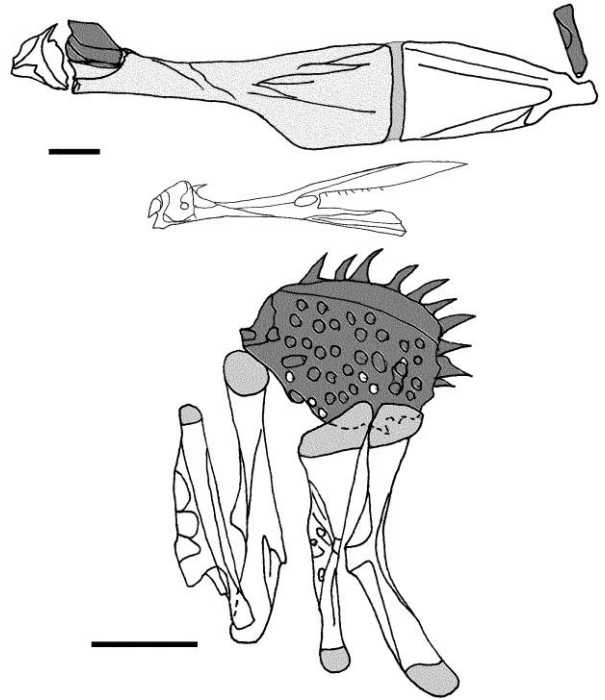


Fig.35. Lateral view of the left hyoid arch (top) and dorsal view of the left dorsal branchial arches (bottom) in *Xeneretmus latifrons* (UAMZ 3196, 95 mm).

The three tightly connected basibranchials are followed by a small cartilaginous element. The hypobranchials are short. The fourth ceratobranchial bears a ventral process. The fifth ceratobranchial is toothed. Epibranchial 1, 3 and 4 bear uncinat processes. Pharyngobranchial 1 is absent. Pharyngobranchial 2 bears a small toothplate. Pharyngobranchial 3 and 4 are absent. In *Anoplagonus*, the third and/or the second basibranchial are absent. In *Tilesina*, *Brachyopsis*, and *Pallasina*, the third basibranchial is absent (Kanayama 1991).

Perciformes

Centrarchidae: *Lepomis gibbosus* (Fig. 36). The basihyal is short. The urohyal consists of an anterodorsal process, a posteriorly bifurcated blade,

a flange in between, and narrow ventrolateral flanges. The hypohyals are not tightly articulated with the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly, is connected to the posterior ceratohyal with medial struts, and bears a large fenestra. The interhyal is cylindrical. Six branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element. Hypobranchials are short. The fourth basibranchial bears a small ventral flange. The fifth ceratobranchial is toothed and bears a ventral flange. Epibranchial 1, 3 and 4 bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears a small toothplate and is connected with a rod-like interarcual cartilage to the first epibranchial uncinat process. Pharyngobranchial 4 is absent, but a toothplate is present.

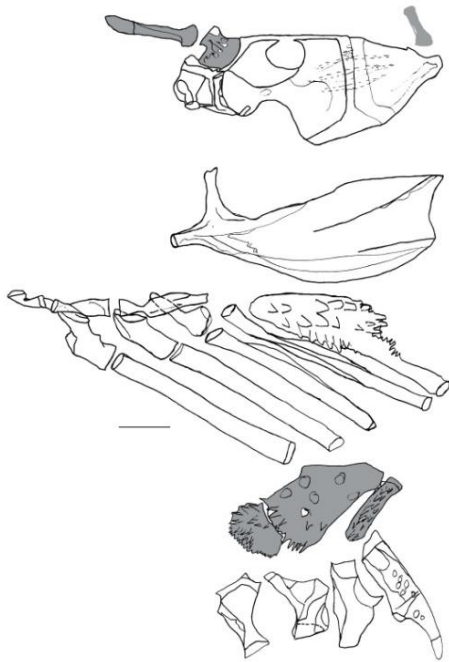


Fig.36. Lateral view of the left hyoid arch (top), urohyal (middle) and dorsal view of the left branchial arches (bottom) in *Lepomis gibbosus* (UAMZ 7715.4, 40 mm).

Percidae: *Perca flavescens* (Fig. 37). The basihyal is cylindrical. The urohyal consists of a blade, a dorsal flange, and narrow ventrolateral flanges. The hypohyals are not tightly articulated with the anterior

ceratohyal and the dorsal hypohyal bears a fenestra. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly and is separated from the posterior ceratohyal, but tiny medial struts are present. The interhyal is cylindrical and long. Seven branchiostegal rays are present.

The three cylindrical basibranchials are followed by a small cartilaginous element. Hypobranchials are short and the first one is angled. The fifth ceratobranchial is toothed and bears a narrow ventral flange. Epibranchial 1, 3 and 4 bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears a small toothplate and is connected to the epibranchial 1 uncinat process by an interarcual cartilage. Pharyngobranchial 4 is reduced and bears a toothplate.

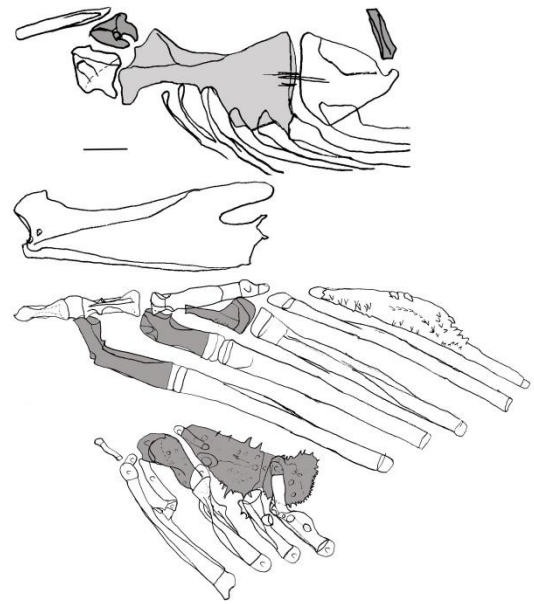


Fig.37. Lateral view of the left hyoid arch (top) and dorsal view of the left dorsal branchial arches (bottom) in *Perca flavescens* (UAMZ 1244, 54 mm).

Cirrhitidae: *Amblycirrhitis pinos* (Fig. 38). The basihyal is cylindrical and relatively long. The urohyal consists of a blade, a dorsal flange, and narrow ventrolateral flanges. The hypohyals are incorporated into the anterior ceratohyal and dorsal hypohyal bears a fenestra. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly and is separated from the posterior ceratohyal. The interhyal is cylindrical and long. Six

branchiostegal rays are present.

The three basibranchials are followed by a small cartilaginous element. Hypobranchial 1 and 2 are short, broad, and bifurcated proximally. The fourth ceratobranchial bears a small ventral flange and the fifth ceratobranchial is toothed and bears a ventral flange. Epibranchial 1, 3, and 4 bear uncinat processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears a small toothplate and is connected to the first epibranchial by an interarcual cartilage. Pharyngobranchial 4 is absent, but a toothplate is present.

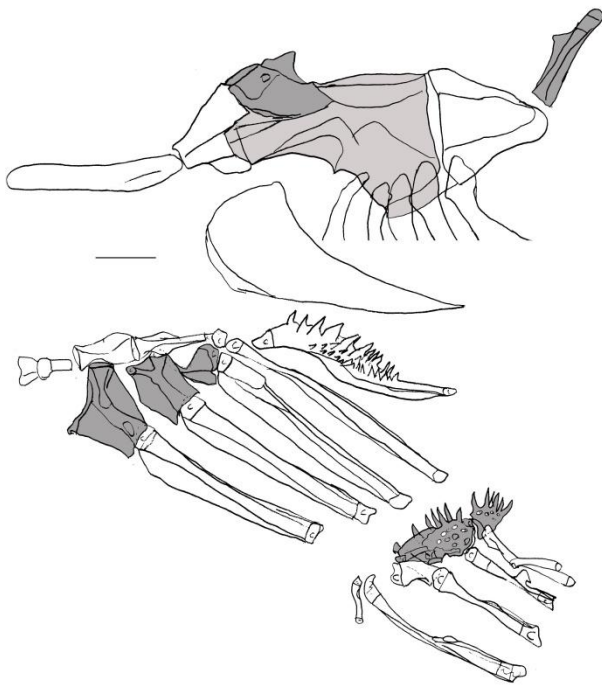


Fig.38. Lateral view of the left hyoid arch (top) and dorsal view of the left dorsal branchial arches (bottom) in *Amblycirrhitus pinos* (UAMZ 3640, 45 mm).

Mugilidae: *Mugil* sp. (Fig. 39). The basihyal is small, but bears a large cartilaginous head anteriorly. The urohyal consists of a blade and a deep ventral and narrow lateral and medial flanges. The hypohyals are small and overlap the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and narrower anteriorly and connected to the posterior ceratohyal via lateral and medial struts. The interhyal is cylindrical. Six branchiostegal rays are present.

The three basibranchials are tightly articulated together cartilaginally, followed by a cartilaginous

element posteriorly, and covered by several small toothplates. The fifth ceratobranchial bears gill rakers and a toothplate. The four short epibranchials bear uncinat processes. Pharyngobranchial 1 is present. An interarcual cartilage connects the second pharyngobranchial with the first epibranchial. Pharyngobranchial 3 and 4 and their toothplates are sutured together. Branchial arches are covered by triangular gill rakers.

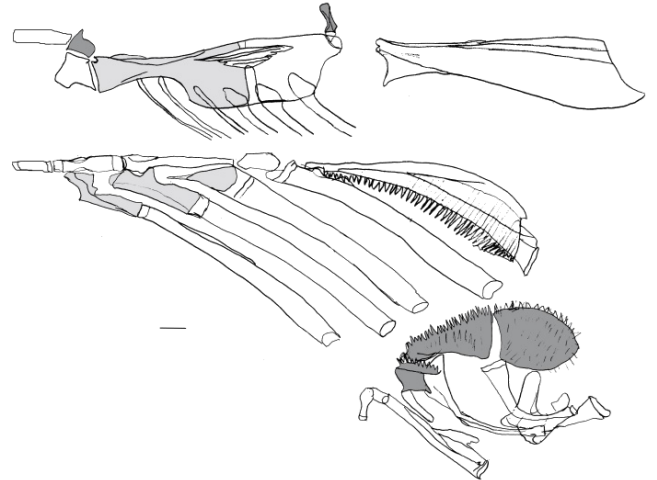


Fig.39. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Mugil* sp. (UAMZ 5125,

Pomacentridae: *Stegastes partitus* (Fig. 40). The basihyal is flattened. The urohyal consists of an anterodorsal process, a posteriorly bifurcated blade, a flange in between, and narrow ventrolateral flanges. The hypohyals are incorporated in the anterior ceratohyal and the dorsal hypohyal bears a fenestra. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly, is connected to the posterior ceratohyal with medial and lateral struts, and bears a small fenestra. The interhyal is cylindrical. Six branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element and the first basibranchial is curved posteriorly and lies ventral to the second one. The hypobranchial are short. The fourth basibranchial bears a small ventral flange. The fifth ceratobranchials are fused together, toothed, and bear posterior extensions. Epibranchial 1, 3 and 4 bear uncinat processes. Pharyngobranchial 1 is present.

Pharyngobranchial 2 bears a small toothplate and is connected to the first epibranchial uncinat process by a rodlike interarcual cartilage. Pharyngobranchial 4 and its toothplate are absent.

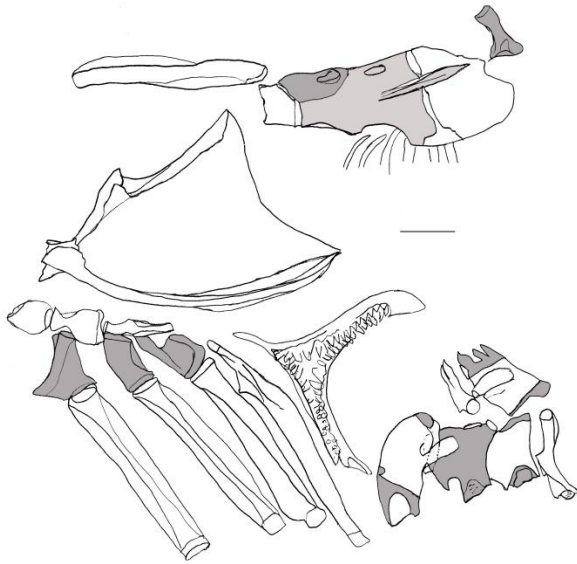


Fig.40. Lateral view of the left hyoid arch (top) and urohyal (middle) and dorsal view of the left branchial arches (bottom) in *Stegastes partitus* (UAMZ 3640, 34 mm).

Acknowledgements

My sincere gratitude would go to late professor J.S. Nelson, Dr. M.V.H. Wilson and Dr. L.R. Parenti for providing helpful comments and advice during the course of this study. I wish to extend my sincere appreciation to Mr. W.E. Roberts, the curator of the University of Alberta Museum of Zoology, the curators and staff of the Smithsonian Institution, California Academy of Sciences, and Australian Museum at Sydney for lending their fish specimens. This study was financially supported by a MCHE scholarship to the author, a NSERC grant to Dr. J.S. Nelson and Isfahan University of Technology.

References

- Baldwin, C.C. & Johnson, G.D. 1996. Interrelationships of Aulopiformes. In: Stiassny, M.L.J.; Parenti, R.L. & Johnson G.D. (eds.), *Interrelationships of Fishes*. Academic Press, San Diego, USA. pp. 355-404.
- Banister, K.E. 1970. The anatomy and taxonomy of *Indostomus paradoxus* Prasad & Mukerji. Bulletin

of the British Museum of Natural History (Zoology). 19: 179-209.

- Bowne, P.S. 1985. The systematic position of Gasterosteiformes. PhD thesis. Department of Zoology, University of Alberta, Edmonton, Canada.
- Bowne, P.S. 1994. Systematics and morphology of the Gasterosteiformes. In Bell, M.A. & Foster, S.A. (eds.), *Evolutionary biology of the Threespine Stickleback*, Oxford University Press, Oxford, UK. pp. 28-60.
- Britz, R. & Kottelat, M. 2003. Descriptive osteology of the family Chaudhuriidae (Teleostei, Synbranchiformes, Mastacembeloidei), with a discussion of its relationships. American Museum Novitates 1-62.
- Collette, B.B. 1966. *Belonion*, a new genus of freshwater needlefishes from South America. American Museum Novitates (2274): 1-22.
- Eschmeyer, W.N. (ed). Catalog of Fishes: Genera, Species, References. <http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>. Accessed October 9, 2014.
- Johnson, G.D.; Baldwin, C.C.; Okiyama, M. & Tominaga, Y. 1996. Osteology and relationships of *Pseudotrichonotus altivelis* (Teleostei: Aulopiformes: Pseudotrichonotidae). Ichthyological Research 43: 17-45.
- Johnson, G.D. & Patterson, C. 1993. Percomorph phylogeny: A survey of Acanthomorphs and a new proposal. Bulletin of Marine Science 52: 554-626.
- Johnson, G.D. & Springer, V.G. 1997. *Elassoma*: another look, In: Abstracts of the 77th ASIH annual meeting, University of Washington, Seattle. p. 176.
- Kanayama, T. 1991. Taxonomy and phylogeny of the family Agonidae (Pisces: Scorpaeniformes). Memoires of the Faculty of Fisheries Hokkaido University 38: 1-199.
- Keivany, Y. 1996. Taxonomic revision of the genus *Pungitius* with emphasis on *P. hellenicus*. MSc. thesis. Department of Biological Sciences, University of Alberta, Edmonton, Canada. 98 pp.
- Keivany, Y. 2000. Phylogenetic relationships of Gasterosteiformes (Teleostei, Percomorpha). PhD. thesis. Department of Biological Sciences, University of Alberta, Edmonton, Canada. 201 pp.

- Keivany, Y. 2014a. Comparative osteology of the jaws in representatives of the eurypterygian fishes. *Research in Zoology* 4(2): 29-42.
- Keivany, Y. 2014b. Comparative osteology of the suspensorial and opercular series in representatives of the eurypterygian fishes. *Iranian Journal of Ichthyology* 1(2): 73-89.
- Keivany, Y.; Nelson, J.S. & Economidis, P.S. 1997. Validity of *Pungitius hellenicus*, a stickleback fish from Greece. *Copeia* 1997(3): 558-564.
- Keivany, Y. & Nelson, J.S. 1998. Comparative osteology of the Greek ninespine stickleback, *Pungitius hellenicus* (Teleostei, Gasterosteidae). *Journal of Ichthyology* 38: 430-440.
- Keivany, Y. & Nelson, J.S. 2000. Taxonomic review of the genus *Pungitius*, ninespine sticklebacks (Teleostei, Gasterosteidae). *Cybio* 24(2): 107-122.
- Kusaka, T. 1974. *The Urohyal of Fishes*. University of Tokyo Press, Tokyo, Japan. 320 p.
- McAllister, D. E. 1968. The evolution of branchiostegals and classification of teleostome fishes. *Bulletin of the National Museum of Canada* (221): 1-239.
- Nelson, G.J. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bulletin of the American Museum of Natural History* 141: 475-552.
- Nelson, J.S. 2006. *Fishes of the world*. Fourth edition. John Wiley & Sons, New York, USA. 601 p.
- Olney, J.E.; Johnson, G.D. & Baldwin, C.C. 1993. Phylogeny of Lampridiform fishes. *Bulletin of Marine Science* 52: 137-169.
- Orr, J.W. 1995. Phylogenetic relationships of Gasterosteiform fishes (Teleostei: Acanthomorpha). PhD thesis. Department of Zoology, University of Washington, Seattle, USA. 813 pp.
- Parenti, L.R. 1981. A phylogenetic and biogeographic analysis of Cyprinodontiform fishes (Teleostei, Atherinomorpha). *Bulletin of the American Museum of Natural History* 168: 335-557.
- Parenti, L.R. 1984. On the relationships of Phallostethid fishes (Atherinomorpha), with notes on the anatomy of *Phallostethus dunckeri* Regan, 1913. *American Museum Novitates* (2779): 1-12.
- Rojo, A.L. 1991. *Dictionary of evolutionary fish osteology*. CRC Press, London, UK.
- Rosen, D.E. 1973. Interrelationships of higher euteleostean fishes. In: Stiassny, M.L.J., Parenti, L.R. and Johnson, G.D.E. (eds.), *Interrelationships of Fishes*. Academic Press, San Diego, USA. pp. 397-513.
- Rosen, D.E. & Parenti L.R. 1981. Relationships of Oryzias, and the groups of Atherinomorph fishes. *American Museum Novitates* (2719): 1-25.
- Rosen, D.E. & Patterson, C. 1990. On Mueller's and Cuvier's concepts of pharyngognath and labyrinth fishes and the classification of percomorph fishes, with an atlas of percomorph dorsal gill arches. *American Museum Novitates* (2983): 1-58.
- Rosen, D.E. & Greenwood, P.H. 1976. A fourth neotropical species of synbranchid eel and the phylogeny and systematics of synbranchiform fishes. *Bulletin of the American Museum of Natural History* 157: 1-67.
- Rosen, D.E. 1984. Zeiforms as primitive plectognath fishes. *American Museum Novitates* (2782): 1-45.
- Stiassny, M.L.J. 1996. Basal ctenosquamate relationships and interrelationships of the myctophiform (Scopelomorph) fishes. In: Stiassny, M.L.J., Parenti, L.R. and Johnson, G.D.E. (eds.), *Interrelationships of Fishes*. Academic Press, San Diego, USA. pp. 405-426.
- Takata, Y. & Sasaki, K. 2005. Branchial structures in the Gasterosteiformes, with special reference to myology and phylogenetic implications. *Ichthyological Research* 52(1): 33-49.
- Taylor, W.R. & Van Dyke, G.C. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybio* 9: 107-119.